

The Opisthobranchs of Cape Arago, Oregon, with Notes on Their Biology and a Summary of Benthic Opisthobranchs Known from Oregon

by

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Abstract. The opisthobranch mollusks from Oregon have not been well studied, and little or nothing is known about the biology of many species. The present study consisted of field and laboratory observations on the biology and ecology of Cape Arago opisthobranchs. Forty-six species were found, extending the range of six northward and two southward. New food records are presented for ten species; 21 species were observed feeding on previously recorded prey. The egg masses of a number of species are described for the first time, and developmental data are given for 21 species. Twenty produce planktotrophic larvae, and *Doto amyra* produces lecithotrophic larvae, the first such example known from eastern Pacific opisthobranchs. *Hallaxa chani*, whose diet consists solely of the sponge *Halisarca* sp., appears to be the first eudoridacean nudibranch known to have a subannual life cycle. Its rapid life cycle appears to be adaptive primarily in exploiting the widely dispersed and fast growing *Halisarca* sp. Data presented on the longevity of *Cadlina luteomarginata* and *C. modesta* suggest they have annual life cycles. Nudibranchs appear to be among the most important predators of intertidal encrusting animals at Cape Arago and probably significantly affect the diversity of the encrusting community. Sixty-six species of benthic opisthobranchs are currently known from Oregon.

INTRODUCTION

THE OPISTHOBRANCH mollusks of Oregon have been little studied compared with those of California to the south and those of the San Juan Archipelago-Vancouver Island region to the north. SOWELL (1949) studied the natural history of opisthobranchs in the Coos Bay-Cape Arago area in the late 1940's and listed 19 species from that area. Since then two relatively brief studies of Oregon opisthobranchs have been made. SPHON (1972) reviewed the literature mentioning Oregon opisthobranchs and reported on a six-day collecting trip made in five Oregon localities. BELCIK (1975) lists species not reported by Sphon that he found in the Coos Bay-Cape Arago area while studying parasites of mollusks and fish. A total of 43 benthic opisthobranchs were reported in these three studies, 21 from Cape Arago.

Members of the order Nudibranchia comprise most of the rocky intertidal opisthobranchs. Although little is known about the biology and ecology of many northeast-

ern Pacific species (BEEMAN & WILLIAMS, 1980), those nudibranchs that have received study have all been shown to be carnivores that prey, as a group, on a wide variety of sessile invertebrates (THOMPSON, 1976; McDONALD & NYBAKKEN, 1978; BEEMAN & WILLIAMS, 1980). Little is known about the effects of their predation on the encrusting animal communities to which they belong.

In this paper I report on observations, scattered over a 45-month period beginning in December 1979 and ending in September 1983, of rocky intertidal opisthobranchs from Cape Arago. The purpose of this research was to (1) determine which species occur at Cape Arago, (2) examine aspects of their biology, including food, feeding methods, larval development, and, in a few cases, life cycles, and (3) attempt to gain some understanding of the effects of nudibranch predation on the encrusting animal community at Cape Arago. Observations are presented for each of the 46 species I found, followed by a general discussion and comments on the benthic opisthobranchs currently known from Oregon.

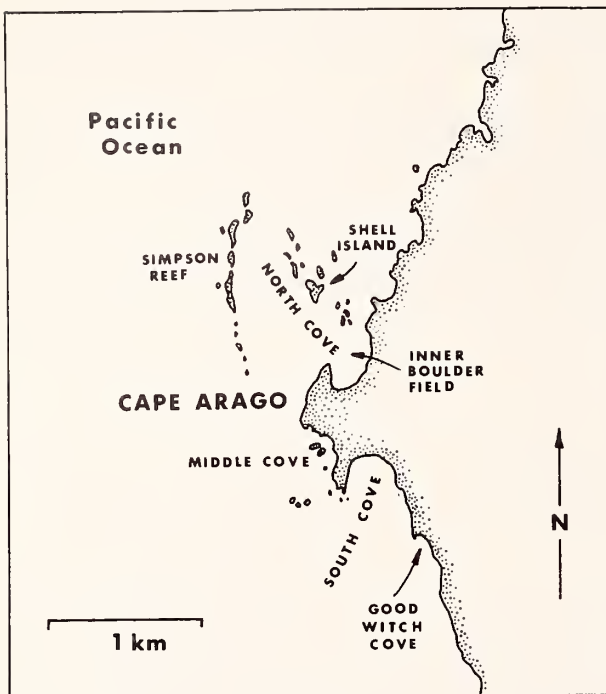


Figure 1

Cape Arago, Oregon (43°20'N, 124°22'W).

STUDY AREA AND DATES OF FIELD OBSERVATIONS

Cape Arago contains one of the widest, most physically and biologically diverse intertidal areas between Cape Mendocino, California, and Cape Flattery, Washington (P. W. Frank and J. J. Gonor, personal communications; personal observations). The study area included North, Middle, and South coves of Cape Arago and one small cove located just south of Cape Arago which I call Good Witch Cove (Figure 1). Cape Arago is situated 7.3 km southwest of the entrance to Coos Bay. Charleston and the Oregon Institute of Marine Biology (O.I.M.B.) are located just inside the south side of the mouth of Coos Bay.

North Cove

North Cove has the largest intertidal area of the four coves. At low tide one can walk beyond Shell Island to the outer boulder field and edge of the *Macrocystis-Nereocystis* kelp bed located just inside Simpson Reef. North Cove contains a mixture of sandstone shelves, outcrops, and boulders of variable size and is protected from large surf by Simpson Reef. Forty-two of 65 trips comprising this study were made to the inner boulder field, one of the most sheltered parts of North Cove (Figure 1). This boulder field consists of roughly half fissured-and-pocketed bedrock and half boulders averaging 0.25 to 0.5 m in

diameter. During the calmer months (spring and summer) much of the inner boulder field is subject to silt and detritus accumulation. Few sea urchins are present, and the area is dominated by the algae *Egregia menziesii*, *Hedophyllum sessile*, *Iridaea flaccida*, *Cystoseira osmundacea*, *Laminaria* sp., the introduced *Sargassum muticum*, and the surfgrass *Phyllospadix*. The undersides of boulders and ledges support a rich variety of sessile invertebrates—the prey of most nudibranchs—and it is under and among these boulders that the greatest number of opisthobranch species and individuals occurring at Cape Arago are found (38 out of the Cape Arago total of 46).

A total of 44 trips was made to North Cove in the following months: 12/'79; 3, 5, 6, 7/'80; 6/'81–5/'82; 8, 9/'82; and 3–9/'83. Trips from 10/'81 to 2/'82 were at night and covered a relatively small portion of the inner boulder field.

Middle Cove

Middle Cove contains the next largest intertidal area of Cape Arago, and, like North Cove, contains a mixture of sandstone bedrock, boulders, and outcrops of varying size. However, Middle Cove is more exposed to surf and possesses a number of invertebrates rare or absent in the North Cove inner boulder field. Among these are the hydrocoral *Allopora porphyra* (Fisher, 1931), the coral-like ectoproct *Heteropora alaskensis* Borg, 1933, and the solitary coral *Balanophyllia elegans* Verrill, 1864. An undescribed white alcyonacean octocoral (see *Tritonia festiva*) is abundant. Where sea urchins are sparse, Middle Cove supports diverse and luxuriant invertebrate and algal communities. Middle Cove appears to possess the highest hydroid and sponge diversity of any of the coves. In ten trips here (made in the months of 3, 7, 8/'80; 6, 8/'81; 5–8/'83) I found 28 species of opisthobranchs.

South Cove

The west side of South Cove consists of a small boulder field semi-protected from surf. As one moves toward the point separating Middle and South coves, surf exposure increases and the substrate becomes solid rock with deep surge channels. Not as many species and individuals of opisthobranchs occur at South Cove. I found 10 species on five trips (2, 5/'80; 5/'81; 6, 7/'82), and none of the species was ever abundant. The low number of opisthobranchs here may be related to the smaller size of the low-intertidal boulder field—much of the area consists of urchin or *Phyllospadix*-dominated bedrock. For unknown reasons, hydroids are rare at South Cove.

Good Witch Cove

This is the most surf-exposed of the coves and is accessible only on the lowest tides when the swell is small. The substrate consists of pocketed-and-fissured bedrock overlain with patches of boulders. Many of these boulders are

relatively barren of organisms—probably the result of grazing by the large numbers of urchins, limpets, and chitons present and perhaps also the result of boulder-overturning by surf. However, the undersides of many ledges and larger boulders support a rich invertebrate fauna. I found 18 opisthobranch species here on six trips (5, 6, 7/'80; 5/'82; 5, 7/'83).

METHODS

Opisthobranch prey species were determined by observing close association of the opisthobranch and its possible prey in the field and by laboratory observation of feeding. Gut contents also were occasionally examined.

Observations on egg masses and larval development were largely restricted to species for which no other data currently exist. To make these observations, opisthobranchs were first separated by species into dishes or jars. A newly laid egg mass was scraped off the side of the container, examined, and transferred to a separate, labelled jar. The water in these jars was changed every one or two days, and all jars were kept in a flowing seawater bath (10 to 17°C). Separated egg masses were examined daily until veligers had hatched, at which time veliger shell lengths were measured. All measurements of eggs and veligers were made with a compound microscope equipped with an ocular micrometer.

Due to the discontinuity of field observations little can be concluded about the seasonality of most of the opisthobranch species. North Cove was observed in every month of the year (though continuously only for one year), and conclusions about seasonality are presented for a few of the species found there. These should be considered tentative.

NATURAL HISTORY OBSERVATIONS

Acanthodoris nanaimoensis O'Donoghue, 1921

This dorid occurred rarely at all four coves. I found a total of seven specimens ranging in length from 5 to 22 mm in February, May, July, and December.

Adalaria sp.

I found ten specimens of this white dorid, ranging in length from 4 to 15 mm in March, April, August, and September at North Cove. Sandra Millen (personal communication) informs me that this is one of three *Adalaria* species found in British Columbia and is not species 138 in BEHRENS (1980). She further states: "It can be recognized by the elongate body, wider at the front end, and by the spicules which project out of the top of the tubercles in a radiating pattern."

Five *Adalaria* sp. were found on the anascan bryozoan *Hincksina minuscula* (Hincks, 1882) on the undersides of boulders. Laboratory observations confirmed that *Adalaria* sp. feeds on this bryozoan. Members of the Onchidoridi-

dae are known to use the radula to open the frontal membranes or opercula of their bryozoan prey and then to use a muscular buccal diverticulum as a pump to suck out the zooids (THOMPSON, 1976). After placing fresh pieces of *Hincksina minuscula* with *Adalaria* sp. specimens for a day, such feeding was evidenced by the many empty zooecia possessing partially attached frontal membranes.

The egg mass of *Adalaria* sp. is a white ribbon laid on edge in a coil of 2 to 4 turns. Egg masses are 1–2 mm high and 4–10 mm in diameter. For data on the larval development of this and other species see Table 1.

Aeolidia papillosa (Linnaeus, 1761)

This eolid is frequent at North Cove. Specimens ranged in length from 5 to 55 mm and often occurred next to *Epiactis prolifera* Verrill, 1869, an abundant anemone upon which *Aeolidia papillosa* readily feeds in the laboratory (personal observation).

Aldisa cooperi Robilliard & Baba, 1972

I found three specimens, one at Middle Cove in June 1981, and two at Good Witch Cove in May and July 1983. The first two were 22 mm and 27 mm long respectively and orange-yellow in color; they had, respectively, 9 and 8 small black spots on the midline of the dorsum between the rhinophores and gills. The third specimen was yellow and also possessed a number of small black spots on the midline.

Aldisa cooperi was originally described as a subspecies of *Aldisa sanguinea*. However, BERTSCH & JOHNSON (1982), on the basis of sympatry, and Millen (personal communication), on the basis of anatomy, consider them to be separate species. With this in mind, I kept one specimen of both species together in a jar to see if mating and egg-laying would occur. The specimen of *A. cooperi* measured 27 mm in length, and that of *A. sanguinea* 20 mm. After one month in captivity (12–16°C), and what appeared to be a number of matings, the specimen of *A. sanguinea* laid an egg mass. The embryos stopped developing at about the 32-cell stage. Although I cannot rule out other factors, this may indicate that interbreeding occurred but resulted in inviable hybrid embryos, thus supporting the conclusion that *A. cooperi* and *A. sanguinea* are distinct species.

Aldisa sanguinea (Cooper, 1863)

One bright-red specimen, 26 mm long and lacking dark spots on the dorsum, was collected at North Cove by the spring 1982 Oregon Institute of Marine Biology invertebrate zoology class. I found another specimen, red-orange in color, 20 mm long, and also lacking dark spots, at Good Witch Cove in May 1983. Specimens of *Aldisa sanguinea* reported from Cape Arago by SOWELL (1949) were red-orange and also lacked dark spots.

Though of weak taxonomic utility, color pattern is the

only character I have used to distinguish *Aldisa sanguinea* from *Aldisa cooperi*. *Aldisa cooperi* is yellow to orange and apparently always has small black spots on the midline of the dorsum (ROBILLIARD & BABA, 1972; BEHRENS, 1980); *A. sanguinea* is red, occasionally yellow-orange to yellow-green, with zero to two relatively large dark spots on the dorsal midline (MCDONALD & NYBAKKEN, 1980). If specimens of *A. cooperi* are found that lack any dark spots, then the identification of the above Cape Arago specimens as *A. sanguinea* will become questionable. More work is clearly needed on these two species. Unfortunately, all I possess of the two specimens of *A. sanguinea* I saw is the radula from the 26 mm specimen.

Ancula pacifica MacFarland, 1905

This species is frequent at North Cove and was most common during spring and early summer. *Ancula pacifica* usually occurred under boulders, and in June 1983 I found eight specimens with egg masses among the entoproct *Barentsia* sp. on the undersides of boulders. Many of these *Barentsia* lacked a calyx—most likely as a result of grazing by *Ancula pacifica*. *Ancula pacifica* is known to feed on *Barentsia ramosa* (Robertson, 1900) in California (MCDONALD & NYBAKKEN, 1978).

Before spring 1983, all the *Ancula pacifica* I had observed at Cape Arago had the color pattern described by ROBILLIARD (1971b) for the two specimens he found in Washington. These specimens lack orange lines on the body but do possess orange-tipped rhinophores, accessory rhinophore papillae, gills, and extrabranchial papillae. In spring and summer 1983 I noticed the above form of *Ancula pacifica* as well as the more typical form (which has orange lines on the body and is common in California) at North Cove. Northern and southern forms of *Ancula pacifica* may exist.

The egg mass of *Ancula pacifica* is a white, slightly flattened, tapering cord. The cord is not laid in a spiral.

Anisodoris lentiginosa Millen, 1982

On 18 May 1980 I found one specimen crawling on bare rock in a pool at Good Witch Cove. It was about 90 mm long, pale yellow in color, and had six small, dark brown blotches scattered on the central part of the anterior two-thirds of the dorsum (Figure 2). This specimen represents a southern range extension of 615 km and is the first intertidal record of the species (MILLEN, 1982).

Anisodoris nobilis (MacFarland, 1905)

Anisodoris nobilis is moderately common at Cape Arago, occurs at all four coves, and can be found all year long at North Cove. I observed specimens less than 10 mm long in December and April. One March specimen measured about 200 mm in length. In the field *A. nobilis* was found feeding on the yellow sponges *Mycale macginitiei* de Lau-

benfels, 1930, *Zygherpe hyaloderma* de Laubenfels, 1932, *Tedania gurjanovae* Koltun, 1958, and *Lissodendoryx firma* (Lambe, 1895). *Anisodoris nobilis* readily feeds on these sponges in the laboratory, and three individuals also ate *Ophlitaspongia pennata* (Lambe, 1895) in the laboratory. *Tedania gurjanovae* and *Ophlitaspongia pennata* are new food records for *A. nobilis* (MCDONALD & NYBAKKEN, 1978; BLOOM, 1981).

On 30 April 1982 I found one *Anisodoris nobilis* about 50 mm long under a boulder feeding on an individual of *Lissodendoryx firma* covering an area of 680 cm² (total boulder undersurface = 4900 cm²). Some of the sponge had already been grazed off the rock. On 21 August 1982 only a few square centimeters of the sponge remained and no individuals of *A. nobilis* (nor any other possible predators of the sponge) were present. Though I cannot rule out that other *A. nobilis* or other predators of *L. firma* had visited the rock, it is possible that the above specimen of *A. nobilis* ate all of the missing sponge.

By area covered, *Zygherpe hyaloderma* is the most abundant of the yellow sponges at North Cove (personal observation). *Mycale macginitiei*, which covers considerably less area (but is a thicker sponge) is next most common. Preliminary observations suggest that *Anisodoris nobilis* prefers *Mycale macginitiei* over *Zygherpe hyaloderma* but will sometimes eat the first of these sponges it contacts, even when the two are in close proximity. Further study of the food preferences of *Anisodoris nobilis* and the effects of length of starvation, previous diet, and age would be interesting.

The ribbon of one egg mass laid by a 140-mm long individual measured 2.7 × 40 cm and contained about 2.1 million eggs.

Aplysiopsis smithi (Marcus, 1961)

This sacoglossan occurred in a few high-intertidal pools between South and Good Witch coves. I examined these pools for *Aplysiopsis smithi* monthly from June 1980 through July 1981. The sacoglossan and its egg masses were abundant in late spring and early summer 1980, and, with the exception of one specimen found in December 1980, disappeared in September 1980 and did not reappear until May 1981. It was abundant until at least July 1981, though not as common as in the previous year. In these pools *A. smithi* feeds exclusively on the green alga *Cladophora* sp. GREENE (1970) reported southern California *A. smithi* feeding on *Cladophora trichotoma*.

My observations of the egg masses and veligers match those of GREENE (1968). He observed white and yellow colored egg masses. I noticed that laboratory specimens laid yellow egg masses at first, but later egg masses were faint yellow to white. The newly hatched planktotrophic veligers lack eyespots and possess a granular black pigment scattered on the edge of the mantle that folds over the outer lip of the shell. Such pigmentation is unique among the veligers observed in this study.

Archidoris montereyensis (Cooper, 1863)

Archidoris montereyensis is fairly common at Cape Arago and occurs year-round. Specimens ranged in length from 4 to 65 mm. Individuals less than 10 mm long were found from November to April, and individuals greater than 50 mm were observed in December, January, April, May, and July. Eggs were observed in the field in May and July. I sometimes found *A. montereyensis* stranded out of water next to or on *Halichondria panicea* (Pallas, 1766) and on the massive and densely spiculate sponge *Suberites* sp. One specimen, 10 mm long, was found at Good Witch Cove embedded in a soft, unidentified, orange, encrusting sponge.

Archidoris odhneri (MacFarland, 1966)

This species is quite common at Good Witch and Middle coves but also occasionally occurs at North and South coves. With the exception of one 13 mm long specimen found in June 1983 at North Cove, all specimens were 70–100 mm long. *Archidoris odhneri* rarely occurred on sponges. Two specimens, including the above 13 mm individual, were on *Hymeniacidon ungodon* de Laubenfels, 1932, and ate this sponge in the laboratory. One 90-mm long specimen, brownish-yellow in color (and the only specimen of *A. odhneri* I found that was not pure white), was found on a large *Suberites* sp. individual of the same color; the sponge appeared to have been grazed. *Archidoris odhneri* has not been reported feeding on either of these sponges (MCDONALD & NYBAKKEN, 1978; BLOOM, 1981).

Berthella californica (Dall, 1900)

This pleurobranchomorph is common on the submerged, relatively barren boulders at Good Witch Cove and also occurs occasionally at the other three coves. BEHRENS (1980) considers *Pleurobranchus denticulatus* MacFarland, 1966 to be synonymous with *Berthella californica* and gives Crescent City, California as the northern range limit of *B. californica*. However, LAMBERT (1976) reported *Pleurobranchus denticulatus* from Pearse Island, British Columbia.

The egg mass of *Berthella californica* is a white ribbon, 3–4 mm wide, laid on edge in a loose spiral. The newly hatched veligers are distinctive in possessing a dark, red wine colored patch of tissue on the right side next to the anus, as well as a shell whose oldest portion has a brown tinge (similar to the pigmentation on the veliger shells of *Hallaxa chani*, but not as dark or extensive).

Cadlina luteomarginata MacFarland, 1966

This species is moderately common at all the coves of Cape Arago. I occasionally found it feeding on the pink sponge *Aplysilla glacialis* (Dybowski, 1880). This sponge has previously been reported as the food of *Cadlina flavo-*

maculata MacFarland, 1905, and *C. modesta*, but not *C. luteomarginata* (MCDONALD & NYBAKKEN, 1978). One individual was found feeding on a light grayish-tan colored *A. glacialis* individual, and a number of *C. luteomarginata* starved in the laboratory fed on *Halisarca* sp. One specimen, 23 mm long at collection, has survived seven months in the laboratory without any food except for one day of feeding on *Aplysilla glacialis* one month after collection.

On 1 May 1982 I noted a specimen of *Aplysilla glacialis* covering an area of 126 cm² on the underside of a North Cove boulder. The boulder had 630 cm² of undersurface. I tagged the boulder to keep track of the sponge. On 21 August 1982 one 27 mm specimen of *Cadlina luteomarginata* and a 15 mm *Cadlina modesta* were observed feeding on this *Aplysilla*. They had eaten 18 cm² of the sponge, but the sponge had grown an approximately equal amount since May. On 26 March 1983 both slugs were still present (though I cannot rule out that they were different individuals or that additional individuals of *Cadlina* had visited the rock) and had eaten all but 4.5 cm² of the sponge. The *C. luteomarginata* measured 42 mm and had laid two egg masses (one recently laid; the larvae of the other had already hatched). The *C. modesta* measured 20 mm. On 15 April 1983 both dorids were gone and only a trace of *Aplysilla* remained.

O'DONOGHUE & O'DONOGHUE (1922:138) stated that the egg masses of *Cadlina luteomarginata* "were not found so frequently as those of *Archidoris montereyensis* and *Diaulula sandiegensis* although the animal itself is quite common," and COSTELLO (1938:331) noted that "the egg ribbons are less vertical than in . . . other forms." My observations agree with both statements. I saw only two egg masses in the field, both in March 1983. The white egg mass ribbon slants toward the center of the tightly wound coil and overlaps itself in the preceding turn. One egg mass had five turns and a diameter of 16 mm. DEHNEL & KONG (1979) described aspects of the egg mass of *Cadlina luteomarginata* but did not mention the angle of the ribbon or tightness of the coil. Egg masses of *C. luteomarginata* may be more common subtidally than intertidally.

Cadlina modesta MacFarland, 1966

Before April 1982 I had only seen two specimens of *Cadlina modesta* at Cape Arago. After April 1982 I found 15 specimens. All 17 specimens were observed in spring and summer at North Cove. Two individuals were feeding on *Aplysilla glacialis* and two on *Halisarca* sp., a previously unreported sponge prey. One individual, 6 mm long and found on *Halisarca* sp., survived in the laboratory at 8–16°C for 17.2 months. This specimen was sporadically fed *Halisarca* sp. for the first 5 months, and grew to 20 mm in length. It was then starved for 6 months. During the following 6 months it was again sporadically given *Halisarca* sp., and it ate a total of 13 cm² of the sponge (*Halisarca* sp. averages 2 to 3 mm in thickness). The specimen

did not appear to eat any of the *Halisarca* sp. present for the last month of its life, and it never laid eggs.

Concerning the color of the rhinophores of *Cadlina modesta*, MACFARLAND (1966) wrote "rhinophores light, seldom dusky," and BERTSCH (1969) stated "the color of the rhinophores varied from whitish to dusky brown." In laboratory specimens of *Cadlina modesta* the rhinophores changed from whitish or light yellow to brown with increasing age.

The egg mass of *Cadlina modesta* is a cream colored ribbon 2–3 mm high laid in a loose spiral of 1 to 3 turns. Mean egg mass area was 115.3 mm² (SD = 52.0, n = 13 egg masses laid in laboratory by three specimens 15–20 mm long). At a mean density of 180 eggs per mm² of egg mass (SD = 33, n = 3), the "average" egg mass of *Cadlina modesta* contains about 20,750 eggs.

Catriona columbiana (O'Donoghue, 1922)

Catriona columbiana is frequent at Cape Arago and was usually on, or near, the stolons of *Tubularia marina* (Torrey, 1902) on which it feeds. *Catriona columbiana* appears to be most abundant in spring and summer, particularly at North and Middle coves. Two color forms exist, one with orange cephalic tentacles and one with white cephalic tentacles (both forms have orange on the distal half of the rhinophores). I did not observe any differences in the radula, mandibles, egg masses, or veligers of these two forms.

This species lays small, sac- to crescent-shaped egg masses (type D of HURST, 1967). There is one egg per capsule, and the capsules are deposited in an irregular coil, 2–3 capsules wide, in the egg mass.

Crimora coneja Marcus, 1961

With the exception of a single specimen reported from "near Humboldt Bay, Humboldt County, California" (McDONALD, 1983), this delicate and rare dorid was previously known only from the type locality of Point Loma, San Diego County, California (BEHRENS, 1980; McDONALD, 1983). On August 29, 1981 Kathryn Young and Tom Wayne of O.I.M.B. collected two individuals from under a boulder in the North Cove inner boulder field (Figure 3). Both specimens were 16 mm long. Since then I have observed seven specimens, ranging in length from 14 to 19 mm, at North Cove (one in December 1981, one in April 1983, two in August 1983, and three in September 1983) and one 12 mm specimen at Middle Cove in July 1983. These eight specimens were on *Hincksina minuscula* on the undersides of boulders approximately 0.3 m in diameter.

Laboratory observations confirmed that *Crimora coneja* feeds on *Hincksina minuscula*. One individual overnight ate almost every zooid in a 1 cm² piece of the bryozoan. The zooecia were empty and the frontal membranes missing, indicating that *Crimora* uses its radula to rasp out entire zooids (in contrast to the feeding method of *Adalaria* sp.).

The egg mass of *Crimora coneja* is a thin ribbon laid flat (not on edge as in most dorids) in a spiral of 4 to 6 turns, and measures 9–12 mm in diameter. The ribbon is about 1 mm wide, contains 1–2 layers of eggs and lacks striations of any sort. In different egg masses the eggs vary from white to pale orange in color. Because of its thinness and form, the egg mass is difficult to discern when laid on bryozoan-encrusted substrates.

Cuthona abronia (MacFarland, 1966)

This eolid can be common during the spring and summer at North and Middle coves. Although occasionally seen crawling on submerged algae or on the surface of calm tidepools, it usually occurs among minute, unidentified, thecate hydroids under boulders in areas subject to little accumulation of silt and detritus (purple sea urchins are often in the vicinity). In April 1982 I found five specimens and about 20 egg masses on the underside of a single small boulder.

Cuthona albocrusta (MacFarland, 1966)

Cuthona albocrusta occurred at Middle Cove (two specimens in August 1980 and four in July 1983) and North Cove (five in May 1980, one in July 1981, and over 11 in July and August 1983). In August 1983 I found five specimens clustered among minute, unidentified, unbranched, thecate hydroids (probably of the family Campanulinidae). These hydroids were partially covered by a fine, light grayish-tan colored silt. The eolids were quite cryptic in this microhabitat.

Cuthona cocoachroma Williams & Gosliner, 1979

Three specimens of this rare eolid were seen at Middle Cove, one in July 1980, one in June 1981, and one in June 1983. The range of *Cuthona cocoachroma* is extended 255 km from Trinidad Head, Humboldt County, California (JAECKLE, 1981). I also found one specimen of *C. cocoachroma* at Cape Blanco (50 km south of Cape Arago) in April 1982.

The egg mass of *Cuthona cocoachroma* is a white cord laid in a small rosette.

Cuthona flavovulta (MacFarland, 1966)

I found seven specimens crawling on submerged algae or on the surface of calm pools at Middle and North coves in summer 1983. The range of *Cuthona flavovulta* is thus extended from Palmer's Point, Humboldt County, California (JAECKLE, 1981).

Cuthona fulgens (MacFarland, 1966)

Four specimens were found crawling on submerged algae or on the surface of calm pools at North and Middle coves in summer 1983. The range of *Cuthona fulgens* is

extended from Duxbury Reef, California (GOSLINER & WILLIAMS, 1970).

Dendronotus frondosus (Ascanius, 1774)

I observed few *Dendronotus frondosus* at Cape Arago until June and July 1983, when over 20 specimens were seen on a small unidentified species of *Obelia* in the very low intertidal of Middle Cove. *Dendronotus frondosus* can be abundant during the spring and summer, feeding on the much larger and highly branched species of *Obelia* on the docks of the Charleston boat basin (personal observations). All Cape Arago specimens were less than 20 mm long, and a number of individuals were on hydroids growing on the brown alga *Cystoseira*. *Dendronotus frondosus* occurred in low numbers at all the coves of Cape Arago.

Dendronotus subramosus MacFarland, 1966

I found only two specimens of *Dendronotus subramosus* at Cape Arago, both at Middle Cove. One specimen, 4 mm long, was under a small boulder, and one 2 mm specimen was on hydroid-covered *Cystoseira*.

Diaphana californica Dall, 1919

One specimen, with a 3-mm long shell, of this minute bullomorph was collected from the North Cove inner boulder field in August 1981. I found three more (shell lengths of 3.3 mm, 3.0 mm, and 2.1 mm) in the same location in September 1983. Much of the mantle and viscera is visible through the thin translucent shell. The range of this species is extended 610 km from Duxbury Reef, California (GOSLINER & WILLIAMS, 1970).

The egg mass of *Diaphana californica* is a fragile and very extensible cord attached to the substrate along its entire length. The cord of one egg mass was laid straight, varied from 0.1 to 0.5 mm in diameter, and measured 20 mm in length. Two other egg masses were C-shaped, with the cord varying from 0.75 to 1.5 mm in diameter; one of these was 7 mm long, the other 10 mm.

Diaulula sandiegensis (Cooper, 1863)

This species is moderately common at Cape Arago and is often seen under ledges and boulders feeding on *Haliclona* sp. A of SMITH & CARLTON (1975:45). Specimens ranged in size from 5 to 70 mm. Specimens less than 15 mm were found in January, March, April, June, and July, and specimens over 50 mm long were found in May through July, and in October and January. Small to medium size individuals are often at the end of a "path" they have eaten into *Haliclona* sp. and, due to the resemblance of their dorsal brown rings or spots to the oscula of the sponge, are quite cryptic. One 40 mm specimen was found in April at North Cove feeding on a buff colored, encrusting species of *Sigmadocia*. This is a new food record for *Diaulula sandiegensis* (MCDONALD & NYBAKKEN, 1978; BLOOM, 1981).

Dirona albolineata Cockerell & Eliot, 1905

This species was abundant at North Cove during the latter part of summer in 1980, 1981, and 1982. It was rare or absent in the other seasons I looked. In 1983 I did not see any until early September, when only two were found. *Dirona albolineata* is usually observed crawling on algae and rocks in pools along with *Janolus fuscus* and *Triopha catalinae*.

Discodoris heathi MacFarland, 1905

I found five specimens ranging in size from 7 to 90 mm during the summer months at North Cove, and one 20 mm individual in August at Middle Cove. An 11 mm specimen found embedded in *Mycale macginitiei* under a boulder ate this sponge in the laboratory. A 60 mm slug ate a 30 mm diameter *Mycale macginitiei* overnight. *Discodoris heathi* has been reported feeding on a number of species of *Mycale* but not *Mycale macginitiei* (MCDONALD & NYBAKKEN, 1978; BLOOM, 1981).

Discodoris heathi lays large yellow egg masses in the typical dorid form.

Doto amyra Marcus, 1961

I observed this species only at Middle Cove: one specimen in July 1980, five in June 1981, and 22 (with egg masses) in May and July 1983.

Despite the taxonomic confusion surrounding eastern Pacific *Doto* species (MARCUS, 1961 described four new species, but BEHRENS, 1980 and MCDONALD & NYBAKKEN, 1980 list only two of those), I am calling this species *Doto amyra* after MCDONALD & NYBAKKEN (1980). With the exception of one, all the specimens I examined matched their description and photograph of *Doto amyra* (Marcus's original description mentions little about the living animal). The cerata cores varied from light yellow to light orange-brown; the gonads were yellow, and the cerata tubercles were translucent white and contained slightly opaque white grains (these grains are larger and less dense than the opaque white grains present in the distal parts of the rhinophores and their sheaths). The exceptional specimen mentioned above, while possessing all the above characteristics, also possessed a subcutaneous black pigment in the body similar to that in the body of *Doto kya*. However, this slug laid eggs identical to those of the other specimens of *Doto amyra*, and, as indicated below, the eggs of *Doto amyra* are very different from those of *Doto kya*.

Most of the specimens of *Doto amyra*, and all of the egg masses, were on colonies of the thecate hydroid *Abietinaria* sp., a previously reported prey of *Doto amyra* (BEEMAN & WILLIAMS, 1980). Slugs occurred on both the stolons and upright portions of the hydroid. Egg masses were usually attached to the bases of the colonies.

Doto amyra feeds on *Abietinaria* sp. by rasping a circular hole in the perisarc with its radula and then sucking out

the hydroid tissues by means of muscular contractions of its esophagus (personal observations). One 5 mm long slug rasped a hole 32 μ m in diameter in the perisarc.

Doto amyra lays yellowish egg masses that are laterally flattened, slightly crescent-shaped with rounded ends, and laid on edge. The thick jelly attachment sheet is translucent white with parallel white striations; the rest of the egg mass jelly is clear. Egg masses measure up to 1.5 mm high by 4 mm long and derive their yellow color from the yellow eggs.

The larvae of *Doto amyra* hatch out as crawling veligers possessing large eyespots, a large foot, a small velum, and poor swimming abilities. In the presence of *Abietinaria* sp., they metamorphose into juvenile slugs within a few days after hatching (personal observation). *Doto amyra* is the first eastern Pacific nudibranch known to produce lecithotrophic larvae (type 2 development of THOMPSON, 1967) (HURST, 1967; THOMPSON, 1967; BONAR, 1978; present study). I will examine this development more closely elsewhere (ms in preparation).

Doto kya Marcus, 1961

In May and June 1980 I found four specimens at North Cove. Two of these were among *Plumularia* sp. and a short unidentified hydroid of the family Campanulinidae. Both hydroids were growing on the perennial portion of the brown alga *Cystoseira*. Three more were seen at Middle Cove in July 1983. All specimens match the photograph of *Doto kya* in BEHRENS (1980).

The white egg masses of *Doto kya* are laterally flattened (more flattened than the egg masses of *Doto amyra*), slightly wavy or folded crescents to semi-circles; they are laid on edge and measure up to 3 mm in length.

Eubbranchus olivaceus (O'Donoghue, 1922)

Two specimens, 6 mm and 8 mm long, were found at North Cove in June and July 1983. The radula from the latter has 42 rows of teeth and does not taper. As MARCUS (1961:49) noted, the nontapering radula is at present the major anatomical character distinguishing *E. olivaceus* from *E. rustyus*.

Eubbranchus rustyus (Marcus, 1961)

I found a few *Eubbranchus rustyus* in the summer months

at North and Middle coves. Six specimens 0.5–5 mm long occurred with egg masses on *Plumularia* sp. at Middle Cove in July 1983. *Eubbranchus rustyus* eats this hydroid in the laboratory (personal observation). The radula from a 6-mm long specimen has 57 rows of teeth and tapers distinctly.

Flabellina trilineata (O'Donoghue, 1921)

Flabellina trilineata is the most abundant eolid at Cape Arago and occurs at all four coves. It is commonly found feeding on *Tubularia marina*, an abundant hydroid at Cape Arago. Both species appear to be most abundant during the spring. I have observed *F. trilineata* feeding on *Eudendrium californicum* Torrey, 1902, in California, and McDONALD & NYBAKKEN (1978) report it feeding on *Eudendrium* sp. Although large *Eudendrium californicum* colonies occur at Middle Cove, often in close proximity to *F. trilineata* and *Tubularia marina*, I never observed the eolid on them. This suggests that *F. trilineata* prefers *Tubularia marina* to *Eudendrium californicum*.

Many individuals of *F. trilineata* lacked orange pigment on the rhinophores and cephalic tentacles. MACFARLAND (1966:321) also noted this variability in color pattern.

Hallaxa chani Gosliner & Williams, 1975

Since first reporting two specimens of *Hallaxa chani* from North Cove, Cape Arago (GODDARD, 1981), I have seen over 70 individuals in the North Cove inner boulder field, and as many as 14 specimens on a single low tide. *Hallaxa chani* is usually on or near its sponge prey *Halisarca* sp. underneath mid- to low-intertidal boulders (Figures 4, 5).

In the laboratory, specimens of *Hallaxa chani* of all sizes readily feed on *Halisarca* sp. and do not feed on the white colonial tunicate (either *Didemnum carnulentum* Ritter & Forsyth, 1917, or *Trididemnum opacum* [Ritter, 1907]) that is common under North Cove boulders and was previously suspected to be eaten by *H. chani* (see GODDARD, 1981). I have never observed *H. chani* feeding on any other organisms.

Hallaxa chani blends well with *Halisarca* sp. (Figures 4, 5). Both organisms are light to yellowish-tan in color, and the reddish-brown flecks and subcutaneous dark spots on *H. chani* match the dark spots on *Halisarca* sp. (The

Explanation of Figures 2 to 6

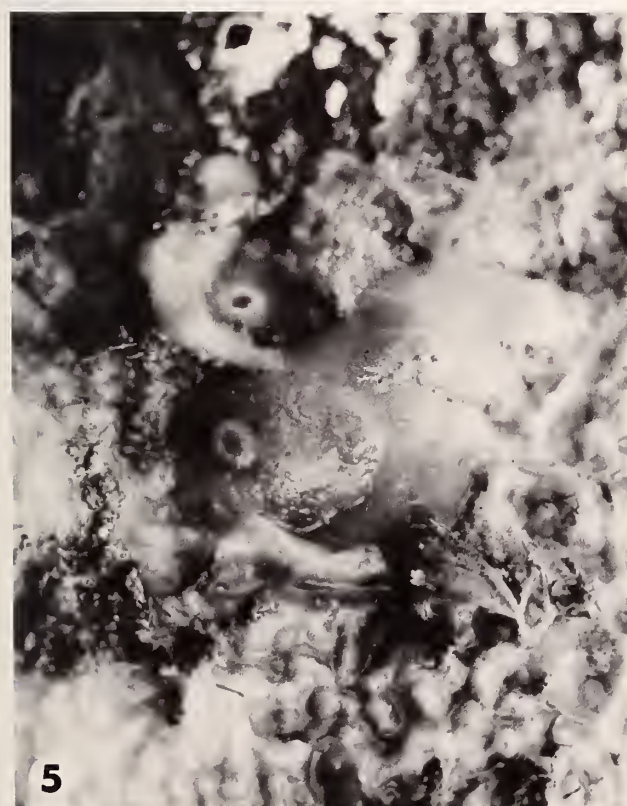
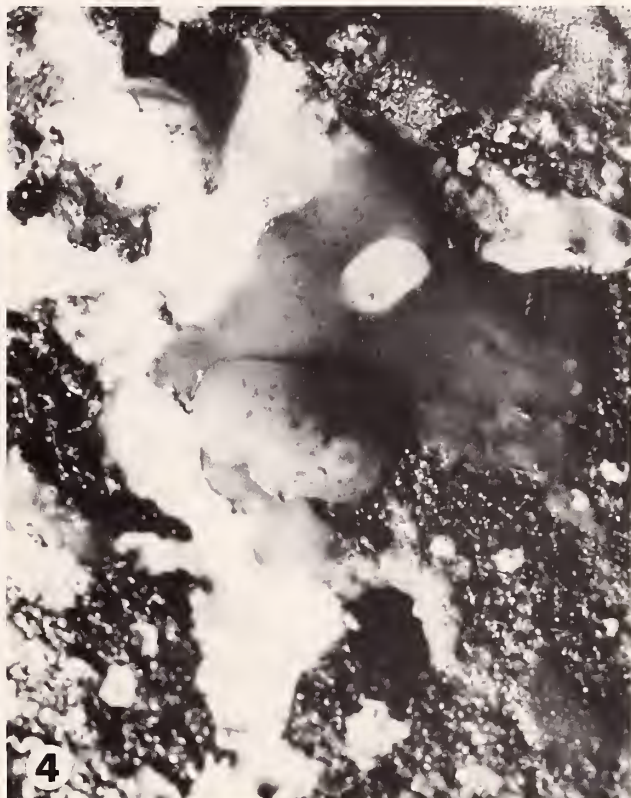
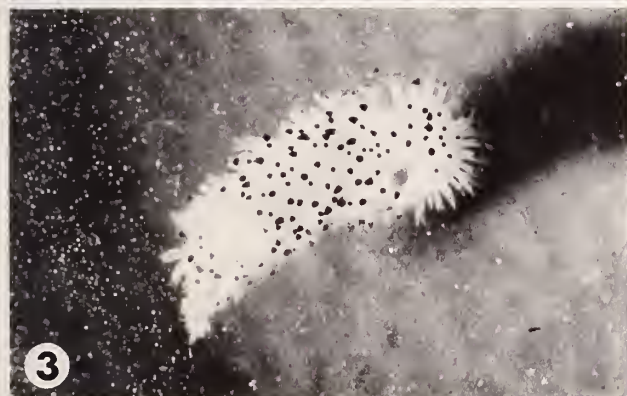
Figure 2. *Anisodoris lentiginosa*, about 90 mm long, found at Good Witch Cove on 18 May 1980.

Figure 3. *Crimora coneja*, 16 mm long, found at North Cove on 29 August 1981 by Katheryn Young and Tom Wayne.

Figure 4. *Hallaxa chani*, about 20 mm long, on *Halisarca* sp. on the underside of a North Cove boulder. 28 April 1982. Note the matching color pattern of the dorid and the sponge. The surrounding white organism is the colonial tunicate *Didemnum carnulentum*.

Figure 5. *Hallaxa chani*, about 18 mm long, on *Halisarca* sp. (center) on the underside of a North Cove boulder. 28 April 1982.

Figure 6. Same spot as in Figure 5, 13 days later. The specimen of *Hallaxa chani* in Figure 5 has eaten all of the *Halisarca* sp., deposited an egg mass, and moved on. 11 May 1982. The small egg mass above the egg mass of *Hallaxa chani* was laid by *Rostanga pulchra*. The sponge in the lower portion of this photograph is *Lissodendoryx firma*; it was subsequently eaten by *Anisodoris nobilis* (see text on *A. nobilis*).



"dark spots" on *Halisarca* sp. are caused by the sponge structure rather than pigmentation. They appear to be associated with the water canal system.) Moreover, when feeding, *H. chani* tends to spread out its semi-translucent dorsum, thus taking on some of the sponge color and also making the thin edge of the dorsum difficult to discern. Small *H. chani* are very cryptic.

Observations indicate that *Hallaxa chani* grows rapidly for a dorid of its size, reaches maturity in a few months, and lives approximately six months. One individual, 5 mm long (wet weight of 20 mg) at collection, kept in 10°C water and given *Halisarca* sp. every few weeks, grew to a wet weight of 360 mg in 44 days, and laid an egg mass 44 days after collection. It weighed 121 mg on day 132, and was moribund after 152 days. Four other specimens of similar initial weight (including one that was kept isolated and never laid eggs but which reached a length of 28 mm and a weight of 957 mg) lived 150 days or less under similar conditions.

The egg mass of *Hallaxa chani* is a cream colored ribbon 2–3 mm high laid in a loose spiral of 1 to 3 turns (Figure 6). The hatching veligers lack eyespots and possess type 1 shells whose oldest portion is a translucent brown color. Specimens of *H. chani* less than 5 mm long occurred in all seasons, and egg masses were found in all seasons except winter, indicating that reproduction occurs most of the year.

Hermaea vancouverensis O'Donoghue, 1924

I found four specimens, 6–8 mm long, of this sacoglossan on brown algae in the North Cove inner boulder field in June 1981.

Hermisenda crassicornis (Eschscholtz, 1831)

Hermisenda crassicornis was not very common at Cape Arago. In June 1981 I found over 20 specimens at Middle Cove, but on other occasions never more than six. Interestingly, *H. crassicornis* is abundant on the docks of the Charleston boat basin during spring and summer. Most of the *H. crassicornis* individuals at Cape Arago and the boat basin are the variety possessing a bluish-white stripe on the cerata (see BEHRENS, 1980:93, lower photograph). *Hermisenda crassicornis* occurs in all four coves.

Janolus fuscus O'Donoghue, 1924

GOSLINER (1982) recently reinstated *Janolus fuscus* as a distinct species from the more southerly *Janolus* (*Antiopeella*) *barbarensis* (Cooper, 1863). Cape Arago *Janolus* are all *Janolus fuscus*, and the *Antiopeella barbarensis* reported from Oregon by SPHON (1972) were undoubtedly also *J. fuscus*.

Janolus fuscus occurred from April to October at North Cove only. During August and September it is one of the most abundant and conspicuous nudibranchs at North Cove. It is usually found crawling on rocks or on the algae

Sargassum and *Egrelia* and the surfgrass *Phyllospadix* in the large pools of the inner boulder field where it searches for the arborescent bryozoans upon which it feeds (McDONALD & NYBAKKEN, 1978; personal observation).

Laila cockerelli MacFarland, 1905

Laila cockerelli was uncommon at Cape Arago until spring and summer 1983 when I found a total of 20 specimens at North and Middle coves. It also occurs at South and Good Witch coves. A number of individuals were observed on the light orange bryozoan *Hincksina velata* (Hincks, 1881) and ate this bryozoan in the laboratory. *Laila cockerelli* has been reported feeding on *Hincksina velata* in California (McDONALD & NYBAKKEN, 1978).

My observations of the pink colored egg mass of *Laila cockerelli* generally match those of O'DONOGHUE & O'DONOGHUE (1922). However, they described it as a "slightly flattened string . . . wound in a close, tight-fitting spiral." Egg masses I observed were a ribbon laid flat in a close spiral. It is very similar in morphology to the egg mass of *Crimora coneja*. One egg mass had 4.5 turns, a diameter of 15 mm, and a ribbon whose width varied from 1.5 to 2.0 mm.

Onchidoris muricata (Müller, 1776)

Onchidoris muricata occurred at North Cove only. I observed specimens in spring 1980, from late summer 1981 to early spring 1982, and again in spring 1983. On two occasions (December 1981 and January 1982) I found over ten specimens; on all other trips six or fewer were seen.

Onchidoris muricata usually occurs under boulders on *Eurystomella bilabiata* (Hincks, 1884) or *Microporella criboosa* (Osburn, 1952), two abundant ascophoran bryozoans which it eats in the laboratory (personal observation). *Onchidoris muricata* that have been feeding on *Eurystomella bilabiata* possess a deep red colored digestive gland visible through the foot. I also found *O. muricata* on *Hincksina minuscula* but did not confirm feeding on this species.

Onchidoris muricata can be difficult to distinguish from *Adalaria* sp. in the field. However, *O. muricata* is usually shorter, rounder, and has bulbous, fairly smooth dorsal papillae. The pointed spicules in the papillae of *O. muricata* barely protrude above the surface of the papillae; those of *Adalaria* sp. protrude very far.

HURST (1967) described the egg mass of *Onchidoris muricata*. Like many other dorids, *O. muricata* sometimes lays only a small portion of an egg coil (personal observation).

Onchidoris sp. (cf. *Onchidoris hystricina*)

This species is referred to as *Onchidoris hystricina* by BEHRENS (1980:66–67), McDONALD & NYBAKKEN (1980:

44–45), BEEMAN & WILLIAMS (1980:328), and McDONALD (1983:198–199). However, *Onchidoris* sp. disagrees with BERGH's 1878 and 1880 descriptions of *O. hystricina*, as well as MARCUS's (1961) description of *O. hystricina*. The dorsal papillae, gills, and radula are very different (Sandra Millen, personal communication; personal observation). The species appears to be undescribed.

Onchidoris sp. was observed only at North Cove and only at the end of summer. I found ten in August 1981, seven in August and September 1982, and six in August and September 1983.

The white egg mass of *Onchidoris* sp. is a cord, 0.75–1.0 mm in diameter, laid in a disorderly spiral of 1 to 4 turns measuring up to 5 mm in diameter.

Placida dendritica (Alder & Hancock, 1843)

I found this species feeding on *Codium fragile* in pools between South and Good Witch coves. BEHRENS (1980) reports San Francisco Bay as the northern limit of this species, but LAMBERT (1976) found it on the northern tip of Vancouver Island, British Columbia.

Polycera atra MacFarland, 1905

Three specimens were observed in September 1983 at North Cove. *Polycera atra* occurred by the hundreds feeding on arborescent bryozoans in the Charleston boat basin in June 1983, but repeated observation in mid-July turned up only a single specimen. The range of *Polycera atra* is extended from Humboldt Bay, California (JAECKLE, 1981).

Precuthona divae Marcus, 1961

This eolid occurred in low numbers at North and Middle coves in the spring and summer. One specimen from Middle Cove was 32 mm long. I have also found *Precuthona divae* at Cape Blanco (50 km south) feeding on the pink colonies of *Hydractinia* sp. The egg mass of *P. divae* is a round, hemispherical rosette. ROBILIARD (1971b) reported egg masses of *P. divae* from San Juan Island, Washington, as being white; those at my study sites were pink.

Rostanga pulchra MacFarland, 1905

Rostanga pulchra is abundant at Cape Arago and occurs with its egg masses throughout the year. I observed it feeding on *Ophlitaspongia pennata* and also found it (and its eggs) on *Antho lithophoenix* (de Laubenfels, 1927) and *Hymedesmia* sp. A (of SMITH & CARLTON, 1975:51). I also found *R. pulchra* close to, but not on, *Plocamia karykina* de Laubenfels, 1927, and *Axocelita originalis* (de Laubenfels, 1930). *Rostanga pulchra* has previously been reported feeding on, or occurring on, all of the above sponges except for *Hymedesmia* sp. A (McDONALD & NYBAKKEN, 1978).

Triopha catalinae (Cooper, 1863)

One of the most common dorids at Cape Arago, *Triopha catalinae* occurs year-round but is most abundant during summer and fall, especially at North Cove. Individuals ranging in size from less than 10 mm to 70 or 80 mm can be found in nearly any month; this suggests a long breeding season and a probable lack of synchrony of reproduction among individuals. I have never seen *T. catalinae* egg masses in the field. Egg masses laid in aquaria are large, pinkish-white, coiled ribbons laid on edge.

At Cape Arago *Triopha catalinae* feeds on unidentified species of arborescent and encrusting bryozoans. Small individuals are often found on bryozoans on the undersides of boulders, and large individuals are usually out in the open, crawling on submerged algae and rocks.

Triopha maculata MacFarland, 1905

I found five orange specimens during summer 1983 at North Cove. All were 10–20 mm long, and three were observed on bryozoans underneath boulders.

Tritonia festiva (Stearns, 1873)

Tritonia festiva occurs at all four coves but is most common at Middle and Good Witch coves. It usually occurs on or near a white to salmon colored alcyonacean octocoral upon which it feeds. SOWELL (1949) also reported finding *T. festiva* "on or near" this octocoral but did not confirm feeding. The octocoral is in the form of low, rounded colonies up to 15 mm in diameter and is undescribed (F. M. Bayer, personal communication). Large aggregations of fairly evenly spaced colonies are common under wave-exposed, low-intertidal ledges at Cape Arago.

The feeding of *Tritonia festiva* on the soft coral is remarkable. The following description is based on observations of 20 feeding attacks made by *T. festiva* 15–25 mm long on soft coral colonies 7–10 mm in basal diameter. While searching for its prey the frontal veil of *T. festiva* is laterally expanded and horizontal. Upon contacting an expanded colony with the sensitive, slender processes on its frontal veil (or with its rhinophores), *T. festiva* pulls back its head, slows its crawling, raises the frontal veil, and begins eversion of its oral canal. The slug crawls slowly and carefully forward, using the tactile sense of the frontal veil and oral canal to position the expanded oral canal over the end of one or a few polyps. Polyps touched by the frontal veil and oral canal contract their tentacles but not their stalks. Once positioned, *T. festiva* rapidly thrusts its head forward while extending its buccal mass. The jaws and radula make a number of strikes in rapid succession, and one to seven polyps are ripped out of the colony as the rest of the polyps quickly contract. Ingested polyps can be seen passing through the esophagus immediately following an attack. *Tritonia festiva* will not attack contracted colonies, probably because they cannot

penetrate the tough and densely spiculate coenenchyme. Every attack I observed was successful.

This feeding process is similar to that described by THOMPSON (1976) for *Tritonia hombergi* Cuvier feeding on *Alcyonium digitatum* (Linnaeus) and is also quite similar (particularly in the positioning phase) to the feeding sequence described by WILLOWS (1978) for *Tritonia diomedea* Bergh, 1894, feeding on the sea pen *Virgularia* sp. *Tritonia hombergi* and *T. diomedea* attain much larger size than *T. festiva* and bite off and ingest pieces of coenenchyme and sections of sea pen respectively. I have observed *T. festiva* biting off only polyps. Large *T. festiva* (or *T. festiva* feeding on small colonies) may bite off pieces of coenenchyme or ingest small colonies.

Tritonia festiva also occurred next to *Clavularia* sp., a stoloniferan octocoral that I observed *T. festiva* eating in the laboratory and which has previously been reported as a prey item of *T. festiva* (MCDONALD & NYBAKKEN, 1978). *Tritonia festiva* from Cape Arago also attacked specimens of *Gersemia rubiformis* (Pallas, 1788) collected from Cape Blanco as well as an unidentified pink gorgonian dredged offshore by local fishermen.

The white egg mass of *Tritonia festiva* is a flattened cord laid in a close spiral and attached to the substrate by a thin, egg-free jelly sheet (type B egg mass of HURST, 1967). The cord is somewhat convoluted, giving the egg mass a rosette appearance. Dimensions are: egg mass diameter, 10–20 mm; height, 1 mm; cord diameter, 0.5 mm. The egg mass is delicate, and the egg capsules are not embedded in a jelly matrix.

DISCUSSION

Life Cycles

Most of the dorid nudibranchs, and all of the eudoridaceans, whose life cycles have been studied have been shown to possess annual life cycles (SWENNEN, 1961; MILLER, 1962; THOMPSON, 1964, 1976; POTTS, 1970; CLARK, 1975; TODD, 1978, 1979; EYSTER & STANCYK, 1981). Dorids known or suspected to possess subannual life cycles are generally smaller, bryozoan-feeding members of the families Corambidae, Goniadorididae, and Polyceridae and the genus *Acanthodoris* (SWENNEN, 1961; MILLER, 1962; CLARK, 1975; PERRON & TURNER, 1977).

Data presented above on the lifespan of *Hallaxa chani* strongly suggest that this eudoridacean is subannual. Combining the observations on lifespan, egg-laying, and larval development, and assuming a one-month planktonic existence and one or two months for the juvenile to reach a length of 5 mm, the generation time appears to be about four or five months at 10°C. It could be shorter at higher temperatures.

The relatively rapid growth and short generation time of *Hallaxa chani* appear to be adaptations for exploiting its sponge prey *Halisarca* sp. A species of *Halisarca* from New Zealand grows rapidly compared to most other sponges and has a generation time of four to five months

(BERGQUIST, 1978). I observed one group of *Halisarca* sp. individuals under a marked boulder at Cape Arago increase in area from 8 cm² to 16 cm² between 29 June 1983 and 7 September 1983 (70 days), and I cannot rule out the possibility that they were preyed upon during this period and thus actually grew more. The North Cove *Halisarca* sp. population is composed of widely distributed individuals averaging only a few square centimeters in area (personal observation). Laboratory and field observations indicate that specimens of *Hallaxa chani* are capable of eating these individuals in a matter of days to weeks (Figures 5, 6).

It is tempting to postulate that natural selection has "traded" spicule production in both *Halisarca* sp. and *Hallaxa chani* for faster growth rates. However, the lack of spicules in *Hallaxa chani* may be adaptive primarily in conferring a textural resemblance to *Halisarca* sp., helping to camouflage the dorid from its predators (GODDARD, 1981). Lacking spicules, *Halisarca* sp. probably has chemical defenses against sponge predators (it does have a pungent odor when torn). Of course, if such defenses do exist in *Halisarca* sp., *Hallaxa chani* and *Cadlina modesta* have been able to overcome them and possibly even use them in their own defense.

Observations on the longevity of *Cadlina luteomarginata* and *Cadlina modesta* suggest that these dorids live at least a year, and thus possess life cycles similar to those known for other eudoridaceans. One *Cadlina modesta* survived a period of starvation longer (and at higher temperatures) than the entire lifespan of regularly fed *Hallaxa chani*. Although this *Cadlina modesta* never laid eggs, observations by THOMPSON (1961), TODD (1978), and EYSTER (1981), as well as the above observations on one *Hallaxa chani* that never laid eggs, all indicate that lack of reproduction can result in larger size, but does not significantly affect lifespan.

Development

Data on the larval development of Cape Arago opisthobranchs are summarized in Table 1. *Aplysiopsis smithi*, *Onchidoris muricata*, and *Triopha catalinae* are the only species in this table whose development has previously been examined (HURST, 1967; GREENE, 1968; BEEMAN & WILLIAMS, 1980).

The development times, egg and veliger sizes, and the production of veligers that lack a propodium, usually lack eyespots, and possess a mantle fold that attaches intermittently to the shell lip all indicate that, with the exception of *Doto amyra*, every species in Table 1 produces planktotrophic veliger larvae (type 1 development of THOMPSON, 1967) (THOMPSON, 1967, 1976). As mentioned previously, *Doto amyra* produces lecithotrophic veligers (type 2 development).

Of the 20 species in Table 1 that produce planktotrophic larvae, four (20%) produce veligers possessing eyespots at hatching. This is rather high considering that the ve-

Table 1
Larval development of Cape Arago opisthobranchs.

Species	Diameter of ova (μm)			Ova per capsule	Embryonic period (days)	Culture temp. ($^{\circ}\text{C}$)	Shell type ⁴	Length of veliger shell ⁵ (μm)		Eye-spots at hatching
	Range ¹	Month ²	N ³					Range ¹	N ³	
<i>Adalaria</i> sp.	81.2–83.7	April	3	1	11	10–12	1	136.0–143.5	3	no
<i>Ancula pacifica</i>	58.3–59.0	June	2	1	9	14–16	1	103.8	1	no
<i>Anisodoris nobilis</i>	83.0	June	1	up to 20	14	14–17	1	152.8	1	no
<i>Aplysiopsis smithi</i>	66.0	July	1	1	7	15–17	1	112.9	1	no
<i>Berthella californica</i>	92.6	May	1	1–2	18	11–14	1	152.7	1	yes
<i>Cadlina modesta</i>	91.0–92.0	April	3	1	16–19	12–15	1	155.6–158.4	4	no
<i>Catriona columbiana</i>	99.7	July	1	1	10	15–17	2	273.9	1	yes
<i>Crimora coneja</i>	71.6–74.2	April	3	1	17–18	10–14	1	115.5–123.5	3	no
<i>Cuthona cocoachroma</i>	96.3	July	1	1	6	15–17	2	256.7	1	no
<i>Diaphana californica</i>	73.2	Sept.	1	1	7–8	12–16	1	122.1–123.6	2	no
<i>Discodoris heathi</i>	76.8	June	1	4–7	15	14–17	1	144.8	1	no
<i>Doto amyra</i>	149.6–154.3	May	4	1	19–21	15–17	1	236.0–238.5	2	yes
<i>Doto kya</i>	~75	July	1	1	7	15–17	1	122.3	1	no
<i>Eubranchius rustyus</i>	92.9	July	1	1	6	15–17	2	240.1	1	yes
<i>Hallaxa chani</i>	79.6–82.6	May	4	1	15–17	11–15	1	147.9–154.1	3	no
<i>Laila cockerelli</i>	95.4	April	1	1	17	10–13	1	141.8	1	no
<i>Onchidoris muricata</i>	75.0–77.3	April	2	1	10–11	7–11	1	128.5–135.6	3	no
<i>Onchidoris</i> sp.	62.6–64.0	Sept.	4	1	9–11	12–16	1	113.3–116.6	4	no
<i>Precuthona divae</i>	107.1	July	1	1	8	15–17	2	249.1	1	no
<i>Triopha catalinae</i>	—	Aug		1	10	14–18	1	~130	1	no
<i>Tritonia festiva</i>	78.9	June	1	1	12	14–17	1	125	1	yes

¹ Range of means. Means calculated from measurements (usually ten) of ova (or veliger shells) from a single egg mass.

² Month in which egg masses laid.

³ N = number of egg masses in which ova (or veliger shell lengths) were measured.

⁴ See HURST (1967).

⁵ Length = longest dimension of shell.

ligers of only one of the 30 northeastern Pacific opisthobranchs studied by HURST (1967) has eyespots at hatching and the statement by THOMPSON (1976) that hatching planktotrophic veligers usually lack eyespots. Planktotrophic veligers develop eyespots before metamorphosis, and species with lecithotrophic or direct development always possess eyespots at hatching (THOMPSON, 1976). As BONAR (1978:187) states "the eyes . . . usually develop rather late in embryogenesis, and along with the appearance of an enlarged propodium signal the approach of metamorphic competence." It thus seems likely that the above four species will be found to possess relatively short obligatory planktonic stages compared to many other species with planktotrophic larvae.

The data in Table 1 generally support THOMPSON's (1976:86) generalization that "within development-type 1, species with the largest eggs have a longer embryonic period, and, moreover, give rise to larger veliger larvae."

Food, Competition, and Aggression

Although most nudibranch species are known to eat a number of prey species (THOMPSON, 1964, 1976; McDONALD & NYBAKKEN, 1978), a few species appear to be monophagous over their entire ranges. Of the species found

at Cape Arago, *Adalaria* sp., *Ancula pacifica*, *Hallaxa chani*, *Laila cockerelli*, and *Precuthona divae*, so far as is known, fit into this latter category (McDONALD & NYBAKKEN, 1978; BEEMAN & WILLIAMS, 1980; GODDARD, 1981; present study). *Crimora coneja* apparently feeds only on *Hincksia minuscula* at Cape Arago, but it is doubtful that this bryozoan occurs in San Diego County, California, one of the other locations where *C. coneja* occurs (OSBURN, 1950). The generalist species at Cape Arago appear to include *Anisodoris nobilis*, *Dirona albolineata*, *Hermisenda crassicornis*, *Rostanga pulchra*, and *Triopha catalinae* (ROBILLIARD, 1971a; NYBAKKEN & EASTMAN, 1977; McDONALD & NYBAKKEN, 1978; BEEMAN & WILLIAMS, 1980; BLOOM, 1981; JAECKLE, 1984; present study). I suspect that most nudibranch species will be found to eat relatively few prey species belonging to a few genera. Data obtained in this study on the prey of Cape Arago nudibranchs are summarized in Table 2. These data are incomplete. With the possible exceptions of *Cadlina modesta*, *Crimora coneja*, and *Hallaxa chani*, more data are needed on the prey of all Cape Arago nudibranchs.

Food data presented in Table 2 for *Anisodoris nobilis*, *Archidoris montereyensis*, *Archidoris odhneri*, *Diaulula sandiegensis*, and *Discodoris heathi* generally agree with data presented by BLOOM (1981, table 2) on the order of sponges

Table 2

Prey of Cape Arago opisthobranchs.

	Prey
Nudibranch species	
<i>Adalaria</i> sp.	<i>Hincksina minuscula</i> *
<i>Aeolidia papillosa</i>	<i>Epiactis prolifera</i>
<i>Ancula pacifica</i>	among <i>Barentsia</i> sp.
<i>Anisodoris nobilis</i>	<i>Mycale macginitiei</i>
	<i>Zygherpe hyaloderma</i>
	<i>Lissodendoryx firma</i>
	<i>Tedania gurjanovae</i> *
	<i>Ophlitaspongia pennata</i> (Lab)*
<i>Archidoris montereyensis</i>	<i>Halichondria panicea</i>
	<i>Suberites</i> sp.
	unidentified orange encrusting sponge
<i>Archidoris odhneri</i>	<i>Hymeniacidon ungodon</i> *
	on <i>Suberites</i> sp.
<i>Cadlina luteomarginata</i>	<i>Aplysilla glacialis</i> *
	<i>Halisarca</i> sp. (Lab)*
<i>Cadlina modesta</i>	<i>Aplysilla glacialis</i>
	<i>Halisarca</i> sp.*
<i>Catriona columbiana</i>	<i>Tubularia marina</i>
<i>Crimora coneja</i>	<i>Hincksina minuscula</i> *
<i>Cuthona abronia</i>	among small thecate hydroids
<i>Cuthona albocrusta</i>	among small thecate hydroids
<i>Dendronotus frondosus</i>	<i>Obelia</i> sp.
<i>Diaulula sandiegensis</i>	<i>Haliclona</i> sp. A
	<i>Sigmatocia</i> sp.*
<i>Discodoris heathi</i>	<i>Mycale macginitiei</i> *
<i>Doto amyra</i>	<i>Abietinaria</i> sp.
<i>Doto kya</i>	among <i>Plumularia</i> sp. and small thecate hydroids
<i>Eubranchius rustyus</i>	<i>Plumularia</i> sp.
<i>Flabellina trilineata</i>	<i>Tubularia marina</i>
<i>Hallaxa chani</i>	<i>Halisarca</i> sp.
<i>Janolus fuscus</i>	arborescent bryozoans
<i>Laila cockerelli</i>	<i>Hincksina velata</i>
<i>Onchidoris muricata</i>	<i>Eurystomella bilabiata</i> *
	<i>Microporella cribosa</i> *
	on <i>Hincksina minuscula</i>
<i>Polycera atra</i>	arborescent bryozoans
<i>Precuthona divae</i>	<i>Hydractinia</i> sp.
<i>Rostanga pulchra</i>	<i>Ophlitaspongia pennata</i>
	on <i>Antho lithophoenix</i>
	on <i>Hymedesmia</i> sp. A
	near <i>Plocamia karykina</i>
	near <i>Axocelita originalis</i>
<i>Triopha catalinae</i>	arborescent bryozoans
<i>Triopha maculata</i>	arborescent and encrusting bryozoans
<i>Tritonia festiva</i>	undescribed alcyonacean octocoral*
	<i>Clavularia</i> sp.
	<i>Gersemia rubiformis</i> (Lab)

Table 2 (Continued)

	Prey
Sacoglossan species	
<i>Aplysiopsis smithi</i>	<i>Cladophora</i> sp.
<i>Placida dendritica</i>	<i>Codium fragile</i>

* New food record.

(Lab) opisthobranch species not found associated with this prey in field, but ingestion of prey observed in laboratory.

most frequently eaten by these dorids in the San Juan Archipelago and further support his general conclusion that "caecate dorids prey on sponges with poorly-organized skeletons and acaecate dorids prey on sponges with well-organized skeletons."

The Cape Arago populations of a number of nudibranchs are clearly not food limited. For example, *Adalaria* sp., *Crimora coneja*, *Laila cockerelli*, and *Onchidoris muricata* all feed on encrusting bryozoans that are abundant at Cape Arago year-round (personal observation), but the nudibranchs themselves are either rare or only sporadically common. It is not known what factors are preventing these species from becoming more abundant. On the other hand, populations of *Cadlina modesta* and *Hallaxa chani* (and *Flabellina trilineata* during periods of high abundance) appear to be much closer to being limited by the abundance of their food. *Aplysilla glacialis* and *Halisarca* sp. are quite scarce; the abundance of *Tubularia marina* fluctuates markedly, possibly as a result of eolid predation.

Large numbers of *Triopha catalinae*, *Janolus fuscus*, and *Dironea albolineata* are found together in the North Cove inner boulder field during late summer and early fall. *Triopha catalinae* and *J. fuscus* feed on arborescent bryozoans (NYBAKKEN & EASTMAN, 1977; McDONALD & NYBAKKEN, 1978; personal observation), and *D. albolineata* eats a wide variety of prey including bryozoans (ROBILLIARD, 1971a). It seems likely that some competition for food occurs between these species during periods of co-occurrence.

When *Janolus fuscus* are crowded in the laboratory they often bite each other, sometimes tearing off and ingesting cerata (Katheryn Young, personal communication; personal observation). I have also observed *Tritonia festiva* taking bites out of each other in the laboratory. In one instance I placed two newly collected specimens of *Tritonia festiva* (20 mm and 35 mm long, collected in June) together in 500 mL of water. Within one day the larger had eaten the smaller specimen. The occurrence of this aggressive behavior and cannibalism has not been documented for either species in the field. It is interesting to note, however, that aggressive behavior between *Tritonia festiva* could be adaptive in reducing feeding interference. As mentioned previously, the alcyonacean prey of Cape

Arago *Tritonia festiva* often occurs in large aggregations of closely and evenly spaced colonies. A feeding attack by *Tritonia festiva* on a colony results in contraction of the remaining polyps of that colony for about two days (personal observation). *Tritonia festiva* will not attack contracted colonies. Feeding interference between *Tritonia festiva* could thus be considerable at high slug densities (i.e., most of the colonies would be contracted). Aggressive behavior between *Tritonia festiva* might be a mechanism for reducing slug density and thus feeding interference.

In *Hermisenda crassicornis*, biting of conspecifics usually follows "sidling" behavior (ZACK, 1975; RUTOWSKI, 1982). Recent work has shown that sidling behavior is actually "alignment for copulation" (LONGLEY & LONGLEY, 1982; RUTOWSKI, 1983). If not simply an attempt to obtain food, the function of the biting that immediately follows mating is obscure. It is possible that biting of conspecifics is also closely related to mating in *Janolus fuscus* and *Tritonia festiva*. Further studies of cannibalism and intraspecific aggression in these species and their relationship to slug density, food density, and size and reproductive state of the slugs are needed.

Triopha catalinae individuals are rarely found in close proximity to one another (NYBAKKEN & EASTMAN, 1977: 282; personal observation), suggesting that aggressive interactions may also occur between individuals of this species. The feeding method of *T. catalinae* (in which whole branches of arborescent bryozoans are ripped off and ingested), and the laboratory observation of a large *T. catalinae* attacking and taking a sizable bite out of a *Laila cockerelli* (personal observation) indicate that *T. catalinae* is physically capable of such aggression. Furthermore, one wonders whether interspecific aggression or predation may occur between *T. catalinae*, *Janolus fuscus*, and *Dirona albolineata*.

Ranges

The range extensions reported above for *Cuthona flavovulta*, *C. fulgens*, and *Polycera atra*, and the occurrence in spring and summer 1983 of the form of *Ancula pacifica* common in California may be related to events associated with the strong El Niño of 1982–1983 (PHILANDER, 1983). These events included above-normal ocean temperatures off the coast of North America (K. T. Briggs, Univ. of California, Santa Cruz, personal communication; A. McGee, Oregon Dept. Fish and Wildlife, personal communication) and probably a weakening and partial reversal of the usually south-moving California current (CHELTON, 1981), as well as an intensification of the near-shore, north-moving Davidson current that occurs in late fall and early winter (BOLIN & ABBOTT, 1963; SCHWARTZLOSE & REID, 1972). If the above species were transported north (as veligers) with these anomalous events, their occurrence at Cape Arago may be brief. On the other hand, they may occur relatively consistently, but in low numbers, at Cape Arago and were previously over-

looked—this appears to be the case for *Crimora coneja*, *Cuthona cocoachroma*, and *Diaphana californica*, all of which were found at Cape Arago before the onset of the above anomalous conditions.

I would like to recommend that dates of observation always be given with range extensions and reports of unusual occurrence. For with increasing monitoring and understanding of coastal hydrographic conditions, it may become possible to explain better the occurrence of many species at the edges of their ranges, or to explain why a species appears in an area for a time and then disappears for long periods. For example, is it possible that the specimens of *Hopkinsia rosacea* reported from Oregon by STEINBERG (1963b) (see below) were carried north (as veligers) from California with the warm waters and currents associated with the intense El Niño of the late 1950's? Mention of the date of observation would have helped evaluate such a possibility. It is interesting that *Eurystomella bilabiata*, the only known prey of *H. rosacea*, is abundant at Cape Arago year-round, but *H. rosacea* is usually absent (personal observation).

The known range of *Crimora coneja* is puzzling. Despite extensive field observation of nudibranchs in central California, only one specimen has been reported between San Diego and Cape Arago (MCDONALD, 1983).

Some Thoughts on the Effects of Nudibranch Predation on the Encrusting Animal Community at Cape Arago

Low-light habitats at Cape Arago (crevices, caves, and the undersurfaces of boulders and ledges) support a diverse encrusting community composed primarily of sponges, bryozoans, colonial tunicates, and cnidarians. The amount of free space varies depending, in part, on the habitat and degree of physical disturbance. For example, the undersurfaces of low intertidal ledges and stable boulders exposed to little sedimentation tend to have little free space, whereas the undersurfaces of boulders exposed to seasonal sedimentation and overturning by waves tend to possess large amounts of free space (personal observation).

As in any community, part of the encrusting animal diversity at Cape Arago can be explained by the spatial complexity of the habitats, coupled with niche diversification and the evolution of habitat selection. However, the coexistence of large numbers of species on relatively uniform surfaces suggests that other factors must be involved in regulating species diversity. Factors that have been implicated in affecting the diversity of other communities and that are probably important at Cape Arago include: predation and disease, fluctuations in the physical and biotic environments, physical disturbance in the forms of sedimentation, boulder-overturning by surf, and erosion (boring clams play a major role in erosion and production of spatial complexity at Cape Arago), and the existence of competitive networks among the encrusting species (CONNELL, 1972, 1978; DAYTON, 1971; HUSTON, 1979;

HUTCHINSON, 1961; JACKSON & BUSS, 1975; PAINE, 1974; SOUSA, 1979). The first three factors can maintain relatively high levels of diversity by preventing competitive equilibrium (at which time competitively inferior species are excluded from the community) from being reached. Of course, at high enough levels, these same factors can keep diversity low. The existence of complex competitive networks can increase the time necessary for competitive exclusion to occur or it could mean that major competitive dominants simply do not exist in the community (JACKSON & BUSS, 1975; JACKSON, 1979; KARLSON & JACKSON, 1981). As CONNELL (1978) and HUSTON (1979) have discussed, a number of these factors probably operate simultaneously in any particular community, with the relative importance of each factor varying in different communities. The observed diversity in a community is, thus, the result of a "dynamic equilibrium" between the growth rates of the component populations and the rates of the above mentioned factors (HUSTON, 1979).

Nudibranchs, which are known to be important predators in some encrusting communities (BLOOM, 1981; CLARK, 1975; DAYTON *et al.*, 1974; RYLAND, 1970; THOMPSON, 1964; and, on the basis of abundance, NYBAKKEN, 1974, 1978), appear to be among the most abundant and important predators of encrusting organisms at Cape Arago (personal observation). Other significant predators of these organisms at Cape Arago include prosobranchs such as *Diodora aspera* (Rathke, 1833) and members of the family Lamellariidae, and probably various chitons, asteroids, and fish (MORRIS *et al.*, 1980; personal observation). Certain flatworms, polychaetes, crustaceans, and pycnogonids are known to eat encrusting animals (MORRIS *et al.*, 1980) and may also be important, especially with regard to predation on newly settled organisms.

Not knowing which encrusting species are competitively dominant at Cape Arago, I cannot say to what extent nudibranchs prey on such species. But, because nudibranchs can eat large amounts of sessile organisms (see data on *Anisodoris nobilis*, *Cadlina luteomarginata*, *C. modesta*, *Crimora coneja*, *Discodoris heathi*, and *Hallaxa chani*) and eat such a wide variety of prey, many of which are among the more abundant species (personal observation), they undoubtedly significantly affect the competitive relationships in the encrusting community at Cape Arago. Some examples of their effects follow.

Other than reducing the abundance of their prey, the most obvious result of nudibranch predation on encrusting communities is the creation of free space available for larval recruitment or intrusion by surrounding organisms. By consuming entire individuals or colonies, nudibranchs can also alter the species composition under a boulder or ledge.

Overgrowth is one of the primary mechanisms of competition between encrusting organisms (JACKSON, 1979). In some cases nudibranchs (and other predators) can erase overgrowth events between encrusting species by preying

on the overgrowing species. This applies to sessile organisms that can be completely grazed off the overgrown species (*i.e.*, certain sponges, tunicates, and perhaps fleshy bryozoans). The sponge *Halisarca* sp. frequently overgrows the bryozoan *Eurystomella bilabiata* at Cape Arago. I have also seen it overgrowing the alcyonacean octocoral prey of *Tritonia festiva*. Twice I have collected *Eurystomella bilabiata* overgrown by *Halisarca* sp. in order to feed the sponge to laboratory *Hallaxa chani*. The dorids grazed the sponge cleanly off the bryozoan, and within a day or two the bryozoan lophophores were extended and feeding. Of course, the viability of the overgrown organism will depend on how long and how extensively it has been overgrown and on its sensitivity to any allelopathic substances made by the overgrowing organism. The large individual of *Aplysilla glacialis* I observed eaten by *Cadlina luteomarginata* and *C. modesta* (see notes on *C. luteomarginata*) had partially overgrown some *Cliona celata* Grant, 1826. The *Cliona celata* appeared healthy after the *Aplysilla* had been grazed away. This is not too surprising, however, considering the shell-boring abilities of *Cliona*; it also suggests that *Aplysilla glacialis* has little or no allelopathic effect on *Cliona celata*.

Partial predation, which results in decreased feeding and reproductive abilities of the grazed organism and can also expose it to settlement by possibly superior competitors (JACKSON & PALUMBI, 1979), is probably widespread. It is inevitable in spatially complex microhabitats where predators cannot reach all of their prey. Moreover, how many predators, given the chance, actually graze all of a sponge or every bryozoan zooid? Some predators are simply not capable of consuming entire colonies (*e.g.*, *Tritonia festiva* feeding on alcyonacean octocorals, and many hydroid-eating eolids that consume the hydranths, but not the stalks and stolons from which hydranths can regenerate). An important question is, how much can a sessile organism lose to predation and still survive with its regenerative abilities?

The feeding of *Tritonia festiva* on alcyonacean octocorals is a vivid example of partial predation. I have observed octocoral colonies being overgrown by *Halisarca* sp., colonial tunicates, and the "social" tunicate *Metandrocarpa taylora* Huntsman, 1912. It would be interesting to compare overgrowth of the octocoral in the presence and absence of *Tritonia festiva*.

The small, abundant dorid *Rostanga pulchra* feeds on the upper layers of orange sponges (personal observation) and appears to be more parasitic than predatory (though more data are needed on its movements, feeding rates, and sponge growth rates). By damaging the sponge, such superficial grazing may increase the sponge's susceptibility to overgrowth or may speed overgrowth interactions already begun. On the other hand, such feeding could possibly facilitate release of allelopathic chemicals and thus slow or prevent overgrowth.

The possible significance of the relationship between nudibranchs and the encrusting community is suggested

in a photograph I have of about 60 cm² of boulder undersurface. The area is completely covered by the bryozoans *Eurystomella bilabiata* and *Hincksina velata* and the sponge *Zygherpe hyaloderma*. Two clumps of an unidentified arborescent bryozoan are growing on the *Hincksina*. *Eurystomella* and *Hincksina* are overgrowing each other in different parts of the area, and the sponge is overgrowing *Hincksina*, but the sponge is also being overgrown by *Eurystomella*. Each of these organisms has at least one nudibranch predator at Cape Arago.

The competitive relationships between encrusting organisms can be very complex. Overgrowth outcomes vary between the same two species and often depend on encounter angle (JACKSON, 1979). Overgrowth may not be complete and certainly does not always result in mortality. Moreover, growth, regeneration, and recruitment rates of the encrusting species all can affect the observed diversity (KARLSON & JACKSON, 1981). If one adds predation (complete and partial) by organisms such as nudibranchs to this already complex system, as well as the other factors affecting diversity previously mentioned, one is left with an extraordinarily complex community for which competitive equilibrium seems unlikely. Rather, there is probably a "dynamic equilibrium," changing on both long and short time scales, between the rates of competitive displacement and the rates at which the other factors act to prevent competitive exclusion (HUSTON, 1979). The observed diversity of intertidal encrusting organisms at Cape Arago results from this dynamic equilibrium and is undoubtedly higher than would exist under a state of competitive equilibrium.

Benthic Opisthobranchs Known from Oregon

The 66 benthic opisthobranch species presently known from Oregon are listed in Table 3. Forty-seven of these have been found at Cape Arago. Twenty-six are new records for Oregon, and 28 are new to Cape Arago. The ranges of *Adalaria* sp. and *Anisodoris lentiginosa* are extended southward, and those of *Crimora coneja*, *Cuthona cocoachroma*, *C. flavovulta*, *C. fulgens*, *Diaphana californica*, and *Polycera atra* northward. Depending on the status of the questionable species listed in Table 3 (see below), the Oregon total could rise to 71 and the Cape Arago total to 49.

Both SPHON (1972) and BELCIK (1975) reported finding a *Pleurobranchus* sp. (Sphon from Strawberry Hill, and Belcik from Cape Arago). These specimens could be different from each other and *Berthella californica*, or one (or both) could be *B. californica*.

The *Trinchesia* sp. (which I have listed as *Cuthona* sp.) reported by BELCIK (1975) on *Tubularia* sp. in the Charleston boat basin could well be *Catriona columbiana*. In my experience in the area, only *Catriona columbiana*, *Flabellina trilineata*, and *Hermisenda crassicornis* occur on *Tubularia marina* (and *Cumanotus beaumonti* on *Tubularia crocea*—see below).

Until the *Eubbranchus* sp. collected by SPHON (1972) can be re-examined, it is impossible to ascertain whether it is an already described *Eubbranchus* species (including one of the two in Table 3) or belongs to an undescribed species.

SOWELL's (1949) report of *Cadlina pacifica* from Cape Arago is questionable. To my knowledge no other specimens of this dorid have been found since BERGH's (1879) description of three specimens collected by Dall in Alaska. Sowell reported finding at least five specimens and does not describe any aspect of them except (p. 22) that they were "always white about the same as the ground color of *Cadlina marginata*." My guess is that these were specimens of *Archidoris odhneri*, a white dorid that was undescribed at the time.

BELCIK (1965) found *Tritonia festiva* and *T. diomedea* (= *T. exsulans*), the two species of *Tritonia* presently known from the Pacific Northwest. It thus seems likely that the "whitish" *Tritonia* sp. he reported dredged off Cape Arago (BELCIK, 1965, 1975) is an undescribed species, possibly that pictured by BEHRENS (1980:103). For this reason I have not listed *Tritonia* sp. under the "questionable species" in Table 3.

BELCIK's (1965) Master's Thesis on the parasitic copepod *Ismaila monstrosa* Bergh contains an appendix listing 32 species of Oregon opisthobranchs that he had examined for parasites. Fifteen of these species were not found by SPHON (1972) and became the basis of BELCIK's 1975 paper. However, BELCIK (1975) includes an additional two species (*Trinchesia* sp., which I have listed as *Cuthona* sp., and *Archidoris odhneri*) that were not mentioned in his Master's Thesis. In addition, the appendix to his Thesis contains one species (*Fiona pinnata*) that Sphon did not find but that Belcik, for some reason, did not include in his 1975 paper. An "*Eolis* sp." is also mentioned in the Thesis and not in the 1975 paper. Presumably this is the same as the *Trinchesia* sp. mentioned above, and thus I have not included it in Table 3. I have included BELCIK (1965) as a reference in Table 3 in order to present the 17 additional species he found but did not include in this 1975 paper. Both BEHRENS (1980) and McDONALD & NYBAKKEN (1980) list Dillon Beach, Marin County, California as the northern limit of *Dirona picta*. However, BELCIK (1975) found it on the docks of the Charleston boat basin. I saw one specimen of *D. picta* collected by the summer 1983 O.I.M.B. invertebrate zoology class. The exact collection location is unknown.

SOWELL (1949) reported finding a form of *Hermisenda crassicornis* at North Cove "among *Laminaria* and *Costaria* and in association with *Triopha carpenteri* and *Dirona albolineata*." He further states "this form appears to be specifically distinct from *H. crassicornis*, but has not been definitely determined." This form is undoubtedly *Janolus fuscus*, which occurs in large numbers in the same habitat as *Triopha catalinae* and *Dirona albolineata*. BELCIK (1975) wrote that Sowell "confused this form with *Coryphella* sp. or *Antipella* spp."

STEINBERG (1963b) recorded Coos Bay, Oregon, as the

Table 3
Benthic opisthobranchs known from Oregon.

Species	Reference*	Occurs at Cape Arago
<i>Acanthodoris hudsoni</i> MacFarland, 1905	2	
<i>Acanthodoris nanaimoensis</i> O'Donoghue, 1921	2, 5, 6, 8	x
<i>Adalaria</i> sp.	8	x
<i>Aeolidia papillosa</i> (Linnaeus, 1761)	1, 4, 5, 8	x
<i>Alderia modesta</i> (Loven, 1844)	4, 5, 8	
<i>Aldisa sanguinea</i> (Cooper, 1863)	1, 8	x
<i>Aldisa cooperi</i> Robilliard & Baba, 1972	8	x
<i>Ancula pacifica</i> MacFarland, 1905	8	x
<i>Anisodoris lentiginosa</i> Millen, 1982	8	x
<i>Anisodoris nobilis</i> (MacFarland, 1905)	1, 4, 5, 8	x
<i>Aplysiopsis smithi</i> (Marcus, 1961)	4, 5, 8	x
<i>Archidoris montereyensis</i> (Cooper, 1863)	1, 2, 5, 8	x
<i>Archidoris odhneri</i> (MacFarland, 1966)	4, 8	x
<i>Armina californica</i> (Cooper, 1863)	3, 5	
<i>Bathydoris</i> sp.	4, 5	
<i>Berthella californica</i> (Dall, 1900)	8	x
<i>Cadlina flavomaculata</i> MacFarland, 1905	1	
<i>Cadlina luteomarginata</i> MacFarland, 1966	1, 4, 5, 8	x
<i>Cadlina modesta</i> MacFarland, 1966	8	x
<i>Catriona columbiana</i> (O'Donoghue, 1922)	2, 8	x
<i>Crimora coneja</i> Marcus, 1961	8	x
<i>Cumanotus beaumonti</i> (Eliot, 1906)	8	
<i>Cuthona abronia</i> (MacFarland, 1966)	2, 8	x
<i>Cuthona albocrusta</i> (MacFarland, 1966)	2, 8	x
<i>Cuthona cocoachroma</i> Williams & Gosliner, 1979	8	x
<i>Cuthona flavovulta</i> (MacFarland, 1966)	8	x
<i>Cuthona fulgens</i> (MacFarland, 1966)	8	x
<i>Dendronotus frondosus</i> (Ascanius, 1774)	1, 2, 5, 8	x
<i>Dendronotus subramosus</i> MacFarland, 1966	8	x
<i>Diaphana californica</i> Dall, 1919	8	x
<i>Diaulula sandiegensis</i> (Cooper, 1863)	1, 2, 5, 8	x
<i>Dirona albolineata</i> Cockerell & Eliot, 1905	1, 2, 5, 8	x
<i>Dirona picta</i> MacFarland in Cockerell & Eliot, 1905	4, 5, 8	
<i>Discodoris heathi</i> MacFarland, 1905	1, 4, 5, 8	x
<i>Doto amyra</i> Marcus, 1961	8	x
<i>Doto columbiana</i> O'Donoghue, 1921	4, 5	x
<i>Doto kya</i> Marcus, 1961	8	x
<i>Elysia hedgpethi</i> (Marcus, 1961)	8	
<i>Eubbranchus olivaceus</i> (O'Donoghue, 1922)	8	x
<i>Eubbranchus rustyus</i> (Marcus, 1961)	8	x
<i>Fiona pinnata</i> (Eschscholtz, 1831)	5, 8	
<i>Flabellina fusca</i> O'Donoghue, 1921	2	
<i>Flabellina trilineata</i> (O'Donoghue, 1921)	2, 5, 8	x
<i>Hallaxa chani</i> Gosliner & Williams, 1975	8	x
<i>Hermæa vancouverensis</i> O'Donoghue, 1924	1, 8	x
<i>Hermisenda crassicornis</i> (Eschscholtz, 1831)	1, 2, 5, 8	x
<i>Hopkinsia rosacea</i> MacFarland, 1905	7	
<i>Janolus fuscus</i> O'Donoghue, 1924	1, 2, 4, 5, 8	x
<i>Laila cockerelli</i> MacFarland, 1905	1, 2, 5, 8	x
<i>Melanochlamys (Aglaja) diomedea</i> (Bergh, 1894)	3, 5	
<i>Melibe leonina</i> (Gould, 1852)	3	
<i>Onchidoris bilamellata</i> (Linnaeus, 1767)	1, 4, 5, 8	
<i>Onchidoris muricata</i> (Müller, 1776)	8	x
<i>Onchidoris</i> sp. (<i>O. hystricina</i>)	8	x
<i>Phyllaplysia taylori</i> Dall, 1900	3, 5	
<i>Placida dendritica</i> (Alder & Hancock, 1843)	8	x
<i>Polycera atra</i> MacFarland, 1905	8	x
<i>Polycera zosterae</i> O'Donoghue, 1924	8	
<i>Precuthona divae</i> Marcus, 1961	8	x
<i>Rostanga pulchra</i> MacFarland, 1905	1, 2, 5, 8	x

Table 3 (Continued)

Species	Reference*	Occurs at Cape Arago
<i>Tochuina tetraquetra</i> (Pallas, 1788)	4, 5	
<i>Triopha catalinae</i> (Cooper, 1863)	1, 2, 5, 8	x
<i>Triopha maculata</i> MacFarland, 1905	8	x
<i>Tritonia diomedea</i> Bergh, 1894	3, 5	x
<i>Tritonia festiva</i> (Stearns, 1873)	1, 2, 5, 8	x
<i>Tritonia</i> sp.	4, 5	
Questionable species		
<i>Cadlina pacifica</i> Bergh, 1879	1	x
<i>Cuthona</i> (<i>Trinchesia</i>) sp.	4	
<i>Eubranchus</i> sp.	2	
<i>Pleurobranchus</i> sp.	2	
<i>Pleurobranchus</i> sp.	4, 5	x

* 1, SOWELL (1949); 2, SPHON (1972); 3, references cited by SPHON (1972); 4, BELCIK (1975); 5, BELCIK (1965); 6, STEINBERG (1963a); 7, STEINBERG (1963b); 8, present study.

northern limit of *Hopkinsia rosacea*. This is the only record of *H. rosacea* north of Abalone Beach, Humboldt County, California (where a single specimen was found—see JAECKLE, 1984). Specimens of *H. rosacea* from Coos Bay were apparently collected by Lawrence Andrews, whom STEINBERG (1963a) cited as her source of opisthobranch specimens from Coos Bay. The only other species STEINBERG (1963a, b) reported from Coos Bay was *Acanthodoris nanaimoensis*.

BELCIK (1975) reported *Alderia modesta* as uncommon on *Vaucheria* mats on mudflats in Coos Bay. At least during the summer, *A. modesta* can be found in abundance feeding on mats of *Vaucheria* sp. in the South Slough of Coos Bay (personal observation).

Five additional species that I have observed in the Coos Bay area, but not at Cape Arago, are *Cumanotus beaumonti*, *Elysia hedgpethi*, *Fiona pinnata*, *Onchidoris bilamellata*, and *Polycera zosterae*. *Cumanotus beaumonti* occurs on *Tubularia crocea* (Agassiz, 1862) in the Charleston boat basin; a single specimen of *E. hedgpethi* was collected in Coos Bay by the summer 1983 O.I.M.B. invertebrate zoology class; *F. pinnata* occurs offshore on floating objects covered with its prey, the gooseneck barnacle *Lepas* sp.; *O. bilamellata* is found among *Balanus glandula* Darwin, 1854, on the pilings and breakwater of the Charleston boat basin; and a single *P. zosterae* was collected from a piling in the Charleston boat basin.

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